A recent advance in evolution

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The locus of evolution

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The locus of evolution

Hoekstra & Coyne 2007:

The locus of evolution: evo devo and the genetics of adaptation

Evolution 61: 995-1016

Why have I chosen this article?

- Recommended by Faculty1000 as….going well with beer….
- I know very little about Evo Devo….or genetics…
- Paper has made significant impact
  - Cited over 50 times last 12 months
  - Two MUST READ recommendations by Faculty1000

Evo Devo

- Relatively new field of evolutionary development
- claims to have ‘revolutionised’ micro- and macroevolution
- Several claims
  - **Idea that the most important evolution involves alterations of the regulation of genes rather than in their structure**

History of Evo Devo

- Jacob 1977: evolution assembles new adaptations by messing around with gene regulations
- King & Wilson 1975: interpreted the similarities in gene and protein sequences between humans and chimps. Suggested that minor changes in gene regulations could yield major phenotypic changes between taxa

History of Evo Devo

- Subsequent work by Wilson & co expand on this view and emphasise gene regulation
- More recent work has focused on the *cis*-regulatory elements
  - Short, non-coding DNA sequences that control the expression of a nearby gene
- Regarded as the site for most important evolutionary change in morphology

History of Evo Devo

- Importance of *cis*-regulation has been emphasised by Carroll
- Evolution of plant & animal form (& other macroevolutionary features) stem largely from changes in *cis*-regulatory sites

cis-regulatory evolution: 2 assumptions

Theoretical: Nature of gene regulation makes promoter elements the most likely sites of evolutionary change. AND changes at the promoter sites are more important to anatomical traits than others (behavioural, physiological, biochemical)

Empirical: cis-regulatory evolution has actually been the most important cause of adaptation

Aim of the paper

- Critically discusses the theoretical assumption underlying the *cis*-regulatory evolution argument
- Tests the empirical assumption that *cis*-regulatory changes have led to the evolution of important morphological traits
  - Survey of literature

Why Form over Function?

- Why do changes in *cis*-regulatory elements only affect morphology and not other types of traits (behaviour, physiology etc)?
- Authors suspect this is largely driven by researchers interested in macroevolutionary changes that can be observed in fossil record
- But is there really an evolutionary difference between making a bone longer or stronger?

Why Form over Function?

- Authors concede that morphology and physiology may evolve at different rates
- BUT:
  - This does not explain why the evolution of morphology is explicitly linked to the regulatory elements of genes and physiology to the coding elements of genes
  - After all, expression of ‘physiological’ and ‘morphological’ genes both involve regulatory elements

Why Form over Function?

- Authors also argue that there are many cases where the function of a gene can not be simply defined as either ‘structural’ or ‘functional’
- Similarly, it is difficult to classify a change within a gene (either at the regulatory or the transcription site) as either affecting structure or function
  - Lots of complicated downstream effects

The theoretical imperative for *cis*-regulatory evolution

- *Evo-Devotees* argue that changes in *cis*-regulatory region leads to more evolutionary change because
- A change in protein sequence (mutation of transcription region) may have deleterious pleiotropic effects - eg. because proteins interact with each other in a network, any changes in sequence could affect interaction)
- Therefore changes in the transcription regions are more likely to be non-adaptive and selected against

The theoretical imperative for *cis*-regulatory evolution

- On the other hand
- Because *cis*-regulatory elements only affect the temporal and spatial expression of a gene, they are thought to be relatively free of negative pleiotropic effects
- Therefore, has a higher probability of being adaptive compared with other random mutation in non-regulatory regions

But

- Hoekstra & Coyne argue that other events are equally or more likely to drive macroevolution
  - Gene duplication
  - Whole genome duplication (47-70% of angiosperms)
  - Alternative splicing sites
- These would also have no deleterious pleiotropic effects as ancestral gene is preserved

…and there is more…

- Rate of fixation of *cis*-regulatory mutations does not necessarily be higher than other mutations
- Eg. if *cis*-regulatory sites at a given gene are less numerous than coding sites, mutation rates are correspondingly lower
- Expressing a protein at a new place or time may be as deleterious as changing that protein

What about the empirical data?

- Evo-Devo asserts that *cis*-regulatory evolution has actually been the most important cause of adaptation
- Extensive literature survey has only found 3 cases of adaptive *cis*-regulatory evolution
  - Two of three involve loss of a trait rather than the origin of new trait

Hoeckstra & Coyne's conclusion

- Too early to say how important *cis*-regulatory regions are for macroevolutionary events

Summary

- Most enjoyable paper
- Easy to follow, even for behavioural ecologists
- Seductive logic has won me over:
  - Down with *cis*-regulatory elements!